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Abstract

A considerable body of work has emerged on the ecology of insectivorous bats in forests of the Pacific Northwest, including dietary studies. Existing research in the Pacific Northwest on bat diets and prey consumption has emphasized populations of bats in Oregon. There are limited data for species inhabiting forests elsewhere in the region. We collected fecal samples from bats captured in mist nets set during May through August, 2004-05, in two watersheds in north-central Idaho that supported forests which were actively managed for timber production. We analyzed fecal samples of 183 bats of five species and compared the results to previously published data for these same species inhabiting forest habitats in the Pacific Northwest. Remains of 12 orders or classes of prey, along with 18 taxonomic families of insects, were identified in the diet of these bats. Prey items included Acari, Arachnida, Coleoptera, Diptera, Hemiptera, Homoptera, Hymenoptera, Isoptera, Lepidoptera, Neuroptera, Orthoptera, and Trichoptera. Based on the percent volume of contents in fecal samples examined, Lepidoptera were the dominant prey of four of the five species of bats examined, with Coleoptera the dominant prey of big brown bats (*Eptesicus fuscus*). Evidence of moderate dietary specialization (> 40% volume of a specific taxonomic grouping) was observed in California myotis (*Myotis californicus*: Lepidoptera), long-legged myotis (*M. volans*: Lepidoptera), and big brown bat (Coleoptera). Comparisons with data for bats in western and eastern Oregon showed major dietary shifts across geographic regions for some species of bats, likely associated with changes in moisture regimes and concomitant shifts in the availability of insect prey. Our data indicate that assemblages of bats living in managed, coniferous forests in Idaho consume a wide range of prey, suggesting that guidelines for management of these habitats should consider the importance of sustaining diverse insect communities to ensure the long-term health of bat populations inhabiting these forests.

Introduction

The ecology and management needs of insectivorous bats inhabiting North American forests has emerged as an important subject of research, confirmed by the number of papers appearing in a wide range of journals and the publication of collective volumes of information on the topic (Barclay and Brigham 1996, Kurta and Kennedy 2002, Lacki et al. 2007b). The forests of the Pacific Northwest have been an especially fruitful region to the study of forest—bat interactions (Hayes 2003) but most of the recently published work on bats in this region comes from Oregon, Washington and northern California, with only limited data available from Idaho.

Recent studies in Idaho of long-legged myotis (*Myotis volans*) have demonstrated the importance of large diameter snags as roosting habitat, both at lower and higher elevations, and have documented extensive use of habitats at mid-elevations for foraging by this species (Johnson 2006). Regardless, data are limited for most species of forest-dwelling bats in Idaho, especially data on diet and prey selection, requiring forest land managers to use databases collected elsewhere when evaluating effects of management on the prey base of bats living in these forest ecosystems.

Dietary studies of bats that inhabit forests have largely emphasized a single or pair of species resulting in an incomplete picture of which arthropods are important to bats in a given area (reviewed in Lacki et al. 2007a). Studies of prey selection by assemblages of bats over large areas or regions do exist for both eastern (Whitaker 1972, Fenton and Bell 1979, Griffith and Gates 1985) and western (Whitaker et al. 1977, 1981a; Warner 1985) populations of North American bats, but few studies have examined in detail the feeding patterns of an assemblage of bats living in a defined locale and subject to the same available

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prey base (Black 1974, Whitaker 2004). Whitaker (2004) found differences in the diets of several sympatric bat species in an Indiana floodplain forest; however, three species of *Myotis* exhibited similar enough diets to suggest that they were using identical foraging strategies in capturing insect prey even though one species, the northern bat (*M. septentrionalis*), is a gleaner (Faure et al. 1993). Given the number of *Myotis* species inhabiting forests of western North America, including the Pacific Northwest, it is plausible to predict that similar patterns exist among assemblages of bats in these areas.

Studies of the food habits of insectivorous bats in the Pacific Northwest exist for eastern (Whitaker et al. 1981a) and western (Whitaker et al. 1977) Oregon, and both studies demonstrate consumption of a wide diversity of insect prey by bats. Whitaker et al. (1981a) concluded that existing data indicate that bats in Oregon exhibit inter-specific partitioning of available food resources. Assemblages of bats in Idaho are likely to be comprised of a different combination of species than studied in Oregon, and, if inter-specific partitioning of food resources by insectivorous bats exists, it is likely that some patterns in diet selection of bats in Idaho should also be different. In this study we examined prey consumption by assemblages of bats inhabiting actively managed, coniferous forests in north-central Idaho. We had three objectives to this study: to describe the range of insect groups eaten by forest-dwelling bats in north-central Idaho, to evaluate whether evidence supports the premise of inter-specific partitioning of food resources by bats in north-central Idaho, and to compare data on prey consumption of these bats to existing studies of the diet of bats in other regions of the Pacific Northwest.

Study Area

This study took place in Clearwater and Latah counties in north-central Idaho, near the town of Elk River. Elk River is surrounded by a topographically diverse landscape that ranges in elevation from 480 to 1,410 m above sea level. Bats were sampled in two watersheds. Watersheds were predominantly forested, consisting of stands of ponderosa pine (*Pinus ponderosa*), grand fir (*Abies grandis*), western red cedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and western larch (*Larix occidentalis*). The area receives 95.5 cm of precipitation annually and has a mean annual temperature of 6.6°C (NOAA 2006); thus, forests are moist in spring and early summer due to the accumulated snowfall in winter, but dry out and become xeric by late June and remain so through July to September due to limited summer rainfall.

Land ownership and, therefore, management is diverse in the region. Most of the land is owned or managed by the Potlatch Timber Company, U. S. Forest Service, U. S. Army Corp of Engineers, or Idaho Department of Public Lands. This variation in land stewards has been associated with different objectives and methods for land management; regardless, much of the land is intensively managed for timber production. Forests owned and managed by Potlatch Timber Company and the U. S. Forest Service include even- and uneven-aged stands created by a variety of silvicultural treatments (Johnson 2006).

Methods

Bats were captured from May to August, 2004 and 2005, in monofilament nylon mist nets placed over water bodies such as "dip ponds" and small streams. Age, sex, forearm length, mass, reproductive status, and species were recorded for all bats captured. After measurements were taken, each bat was held in a small cloth bag for ca. 15 min to collect feces for dietary analysis. All methods used in handling bats were approved by the University of Kentucky Institutional Animal Care and Use Committee (IACUC No. 00219A2001).

Fecal samples were labeled and stored in a freezer until they could be analyzed in lab. Pellets were dissected as described by Whitaker (1988) and prey remains identified to class, order or, when possible, the family level. We estimated percent frequency of prey items in the diet among individuals for each species of bat, and estimated the percent volume of prey items in pellets from each bat to the nearest five percent. Up to three pellets were dissected from each bat, and average values across pellets were used in determining percent volumes of prey in the diet. We compared data among species and between age classes of bats within species.

We searched for possible geographic trends in selection of major prey groups by bats in the Pacific Northwest by comparing data for bats from north-central Idaho with published results of bats inhabiting arid (≤ 30 cm of rainfall year^{-1}) pine forests on the leeward side of the Cascade Range in eastern Oregon (Whitaker et al. 1981a), and coastal wet (ca. 95–195 cm of rainfall year^{-1}) coniferous forests on the windward side of the Cascade Range in western Oregon (Whitaker et al. 1977). We tested for differences in major prey groups among regions using species of bats as blocks with Friedman's Distribution-Free tests, and evaluated differences among regions with distribution-free multiple comparisons based on Friedman Rank Sums (Hollander and Wolfe 1973).

Results

We collected fecal samples from 183 bats and five species and identified remains of 12 classes or orders of prey, including 18 taxonomic families of insects in the diet of these bats (Table 1). Three other species of bats were captured infrequently so no attempt was made to assess diet of these species, including little brown myotis (*Myotis lucifugus*; n = 1), fringed myotis (*M. thysanodes*, n = 2), and hoary bat (*Lasiurus cinereus*, n = 1).

Based on both the percent volume and percent frequency of contents in the fecal samples examined, Lepidoptera was eaten the most by four of the five species of bats captured (Table 1), with Coleoptera the dominant prey of big brown bats (*Eptesicus fuscus*). Evidence of moderate dietary specialization (> 40 % volume of a specific taxonomic grouping) was observed in California myotis (*Myotis californicus*: Lepidoptera), long-legged myotis (*M. volans*: Lepidoptera), and big brown bat (Coleoptera). The western long-eared myotis (*M. evotis*) had the most diverse diet with all 10 orders of insects recorded as prey appearing in fecal samples of these bats, along with Acari and Arachnida. Diets of the three species of *Myotis* examined were largely similar in that each species ate a variety of insect orders, but all three relied heavily on Lepidoptera followed by Coleoptera as their primary insect prey.

Geographic trends in diet were compared using these data and published data for these same five species of bats from western and eastern Oregon, with major shifts in diet evident for several species among regions (Table 2). California myotis rely heavily on Dipterans in their diet in coastal wet forests of western Oregon, but switch to eating primarily Lepidopterans in inland forests. Dipterans are also a major component of the diet of silver-haired bats (*Lasionycteris noctivagans*) in coastal wet forests, but are eaten to a lesser extent by these bats in inland forests. Big brown bats feed on Coleopterans and, to a lesser extent Lepidopterans, in all three forested regions showing limited variation in diet among regions. In contrast, western long-eared myotis and long-legged myotis feed most extensively on Lepidopterans regardless of the geographic region sampled.

Variation in the importance of major prey groups was evident for Dipterans ($S = 5.2$, $P = 0.09$) and Coleopterans ($S = 7.6$, $P = 0.02$); however, multiple comparison tests among regions demonstrated a difference only for Coleopterans ($P = 0.04$), with beetles less important to the diet of the assemblage of bats inhabiting coastal wet forests in western Oregon than in inland mesic forests in north-central Idaho. Bats in north-central Idaho, particularly California myotis, western long-eared myotis, and long-legged myotis, appeared to exhibit a greater reliance on Coleopterans in their diet than did these species in either western or eastern Oregon. These data likely suggest that regional differences exist in the availability of insect prey across forests of the Pacific Northwest.

Discussion

Bats in north-central Idaho demonstrated diversity in diets similar to that observed in other regions of the Pacific Northwest (Whitaker et al. 1977, 1981a) and western North America (Black 1974, Warner 1985). The diet of big brown bats was comprised largely of Coleopterans, consistent with data for this species throughout its distribution (Brigham and Saunders 1990, Whitaker 1995, Hamilton and Barclay 1998). Diet of silver-haired bats in north-central Idaho was diverse with some evidence to suggest an emphasis on Lepidopterans. Data for this species in Oregon indicate the same patterns (Whitaker et al. 1977, 1981a, 1981b).

Our data showed that four of the five species of bats sampled in north-central Idaho relied more on Lepidopterans in their diet than any other prey taxa, suggesting that competition for moth prey likely exists. Regardless, because consumption of moths was only examined at the ordinal level we cannot state whether inter-specific partitioning of food resources among species of bats in this assemblage occurs, even though such a pattern has been suggested for other bat assemblages in

TABLE 1. Percent volume and percent frequency of prey in fecal samples of bats in north-central Idaho, 2004–05. Numbers of bats are in parentheses.

Item	*Eptesicus fuscus* (7) % vol.	*Eptesicus fuscus* (7) % freq.	*Lasionycteris noctivagans* (24) % vol.	*Lasionycteris noctivagans* (24) % freq.	*Myotis californicus* (45) % vol.	*Myotis californicus* (45) % freq.	*Myotis evotis* (39) % vol.	*Myotis evotis* (39) % freq.	*Myotis volans* (68) % vol.	*Myotis volans* (68) % freq.
Acari	<0.1	28.6			<0.1	6.7	0.1	7.7	<0.1	4.4
Arachnida							0.4	5.1		
Coleoptera										
Unknown	35.4	71.4	5.8	54.2	13.9	75.6	20.6	74.4	30.7	100.0
Carabidae							2.5	12.8	0.1	5.9
Scarabaeidae	6.4	28.6			0.3	4.4	2.5	5.1	0.1	5.9
Chrysomelidae	3.6	14.3	2.7	16.7	3.1	28.9	1.9	15.4	0.3	14.7
Diptera										
Unknown			1.6	25.0	2.9	35.6	3.2	38.5	1.8	29.4
Chironomidae					0.2	2.2	0.3	2.6		
Muscoidea							0.1	2.6	0.7	1.5
Tipulidae			1.8	12.5	0.3	2.2			0.1	2.9
Sciaridae					0.4	6.7	1.2	10.2		
Psychodidae			0.1	4.2			0.4	2.6		
Rhagionidae					0.1	2.2				
Culicidae	1.7	14.3			0.3	4.4	0.4	2.6	0.1	4.4
Hemiptera										
Unknown	1.9	14.3	2.1	20.8	2.2	22.2	5.2	30.8	3.3	50.0
Lygaeidae	1.2	28.6	10.8	50.0	3.0	20.0	5.6	25.6	1.8	35.3
Pentatomidae			1.2	4.2						
Homoptera										
Unknown	1.0	28.6	1.0	8.3	<0.1	2.2	0.6	5.1	0.1	4.4
Cercopidae	9.5	28.6	1.4	12.5						
Cicadellidae	2.9	14.3	7.1	45.8	0.3	2.2				
Hymenoptera										
Unknown			0.2	8.3	1.4	13.3	0.9	15.4	1.1	14.7
Ichneumonidae					0.8	4.4	0.5	5.1		
Formicidae			0.7	4.2						
Isoptera					0.1	2.2	0.5	2.6		
Lepidoptera	23.8	100.0	38.2	100.0	50.8	100.0	36.5	92.3	49.2	100.0
Neuroptera										
Unknown			2.4	29.2	1.1	11.1	1.2	15.4	1.3	22.0
Chrysopidae					3.6	26.7			1.7	10.3
Hemerobiidae	1.2	14.3	7.0	37.5	0.6	2.2	4.5	20.5	0.5	5.9
Orthoptera	1.0	14.3	0.7	12.5			2.7	10.2		
Trichoptera	6.2	42.9	7.9	50.0	12.2	71.1	6.4	38.5	2.9	27.9
Other[a]	4.3	57.2	7.1	83.7	2.4	37.8	1.9	56.6	4.0	61.7

[a]Includes hair, plant material, and unidentified items.

both western (Black 1974, Whitaker et al. 1977, 1981a) and eastern (Whitaker 1972, 2004; Griffith and Gates 1985) North America. Evidence for moderate dietary specialization on Lepidoptera was present for California myotis and long-legged myotis, as each species consumed moth prey at >40 % volume in the diet (Lacki et al. 2007a). Whitaker et al. (1981a) observed similar patterns for these species in eastern Oregon, but data for California myotis in western Oregon demonstrated a much lower percent volume of moths in the diet of these bats (Whitaker et al. 1977).

TABLE 2. Consumption of major food items (% vol.) by bats across a longitudinal gradient of coniferous forests of differing moisture conditions in the Pacific Northwest.

Bat species/ Prey item	Western Oregon[a] coastal wet forests	Eastern Oregon[b] inland xeric forests	North-central Idaho inland mesic forests
Eptesicus fuscus			
Diptera	15.9	8.0	1.7
Coleoptera	34.4	37.8	45.4
Homoptera	1.5	9.8	13.3
Lepidoptera	21.3	24.1	23.8
Lasionycteris noctivagans			
Diptera	18.9	9.8	3.6
Coleoptera	2.7	1.6	8.5
Homoptera	3.4	2.6	9.4
Lepidoptera	32.0	64.4	38.2
Myotis californicus			
Diptera	60.2	18.4	4.1
Coleoptera	0.3	7.8	17.3
Homoptera	0.6	4.7	0.4
Lepidoptera	14.4	52.0	50.8
Myotis evotis			
Diptera	12.3	11.2	5.6
Coleoptera	18.0	6.1	27.5
Homoptera	1.2	2.0	0.6
Lepidoptera	46.2	58.6	36.5
Myotis volans			
Diptera	1.6	6.9	2.8
Coleoptera	-	4.7	31.2
Homoptera	1.8	1.0	0.1
Lepidoptera	78.2	77.9	49.2

[a] Data are from Whitaker et al. (1977) and are percent volume of stomach contents.

[b] Data are from Whitaker et al. (1981a) and are percent volume of fecal samples.

Our data indicated that diets of the three species of *Myotis* captured most frequently, California myotis, western long-eared myotis and long-legged myotis, were fairly consistent across prey consumed regardless of these species' foraging strategies or use of habitats. Whitaker (2004) observed a pattern comparable to this among three species of *Myotis* feeding along a riparian corridor in Indiana. One of these species, the northern bat, is a gleaner (Faure et al. 1993) and, therefore, was anticipated to demonstrate dietary variation when compared to the other two *Myotis* species. This absence of variation led Whitaker (2004) to suggest that perhaps most all *Myotis* species glean prey at times, some are just better adapted to it than others. Among the three species of *Myotis* we captured most often in north-central Idaho, the western long-eared myotis is a gleaner (Faure et al. 1990, Faure and Barclay 1992); thus, we anticipated that it also should have demonstrated differences in diet when compared with sympatric *Myotis* species. Western long-eared myotis did eat some taxa more typical of gleaners and not found in the diet of the other *Myotis* species we sampled, Arachnids and Orthopterans, but the amounts of these two prey items eaten by these bats were slight and the overall diets among the three *Myotis* species were largely comparable. Western long-eared myotis are known to feed along forest paths in western North American forests (Barclay 1991). This pattern is also evident in data from mist net captures of northern bats in forests in eastern North America (Lacki and Hutchinson 1999).

Comparison of data on prey consumption of five species of bats in Idaho with the same species in western and eastern Oregon demonstrated that Diptera are important in the diet of bats inhabiting coastal wet forests west of the Cascade Range. In contrast, even though Lepidoptera was eaten at the greatest percent volumes of any insect order by most species of bats in north-central Idaho, Coleopterans were also eaten at levels significantly greater than displayed by these species in western Oregon. These data suggest that forest-dwelling bats in the Pacific Northwest may switch from a reliance on Dipterans to Coleopterans as major components of their diet when faced with more xeric habitat conditions and, likely, associated differences in the availability of insect prey between mesic and xeric forest habitats.

Do these patterns represent "true" differences in prey consumption of bats across regions of the Pacific Northwest? We believe they do because samples in Whitaker et al. (1977, 1981a) were collected from throughout their respective regions, data for all three studies are based on large sample sizes of bats (Range: 183–949), and all three studies covered 2-4 years of sampling, removing annual variation in abundance of insect prey as an explanation for the differences observed. Differences in methodology among the studies do exist as Whitaker et al. (1981a) examined stomach contents, Whitaker et al. (1977) examined stomach and fecal samples, and this study examined only fecal samples. It is has been demonstrated, though, that the two methods can yield equivalent results leading to the same order of importance of prey items in the diet (Kunz and Whitaker 1983).

The relevance of these patterns goes beyond simply describing the ecology of these bats, but demonstrates the need to perform dietary studies of bats in multiple locations and habitats in order to fully understand the complete range of responses that bats have to differing availabilities of insect prey. Although some data on abundance of insect prey are available for the study area in north-central Idaho in 2005 (Johnson 2006), no data on insect abundance accompanied either of the studies in Oregon (Whitaker et al. 1977, 1981a). Thus, actual selection from among available prey by bats cannot be assessed. Regardless, patterns in prey consumption among species of bats, which are consistent within a region, but vary across regions, are suggestive of geographic differences in either insect availability and/or bat behavior. Such information has relevance to forest management practices that alter forest structure, plant composition, and water quality, as all of these will impact habitat available to insect prey. Sound stewardship of forest resources suggests that silvicultural practices be evaluated and modified, if necessary, to ensure that habitat conditions favorable to the production of insect prey of bats be maintained (Guldin et al. 2007, Hayes and Loeb 2007). This recommendation is especially applicable to north-central Idaho, where the number of land stewards present in the region is high, and where the levels of timber extraction have been extensive and are likely to remain so into the foreseeable future.

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